

## Can paleorefugia of cold-adapted species in talus slopes resist global warming?

Vlastimil Růžička<sup>1)</sup>, Miloslav Zacharda<sup>2)</sup>, Petr Šmilauer<sup>3)</sup> and Tomáš Kučera<sup>3)</sup>

<sup>1)</sup> Institute of Entomology, Biology Centre, Czech Academy of Sciences, Branišovská 31, CZ-370 05 České Budějovice, Czech Republic (corresponding author's e-mail: vruz@entu.cas.cz)

<sup>2)</sup> Vodňanská 19, CZ-370 05 České Budějovice, Czech Republic

<sup>3)</sup> Faculty of Science, University of South Bohemia, Branišovská 31, CZ-370 05 České Budějovice, Czech Republic

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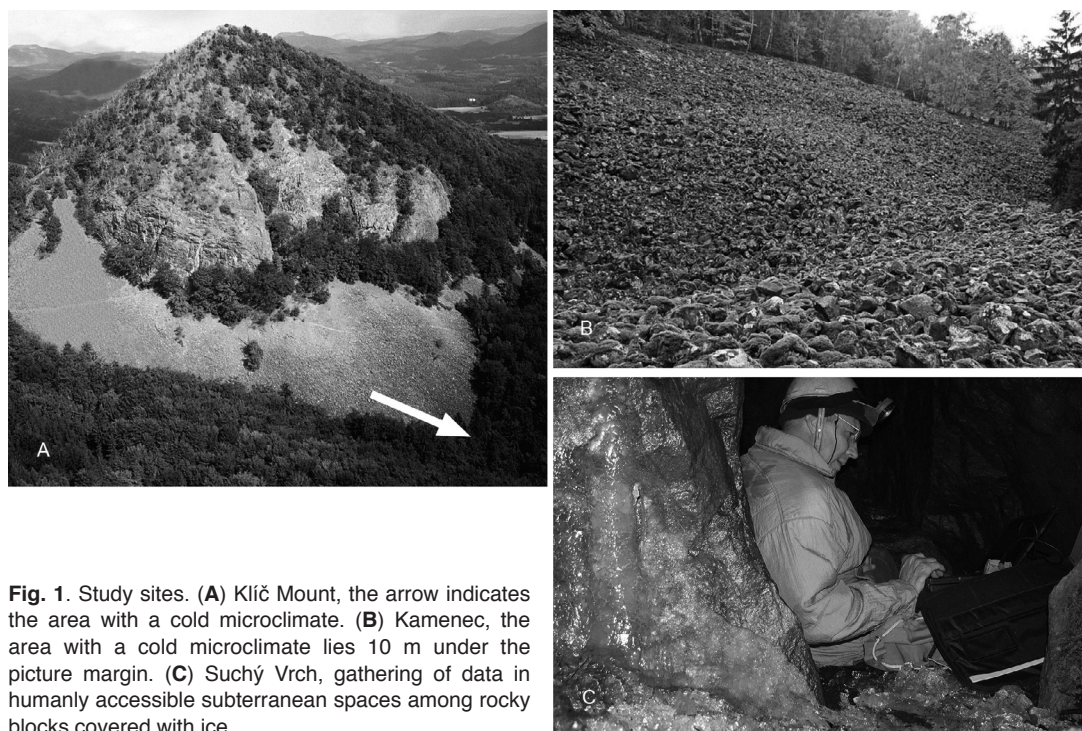
In central Europe, some boreal and arctic organisms can survive in low-altitude freezing talus slopes disjunct from their normal ranges far to the north. The external air temperature and the interior temperature of the talus were measured for five years at three low-elevation talus slopes in North Bohemia (Czech Republic). The year-round interplay between both temperature regimes was affected both by below-average as well as above-average climatic variations during winters 2005–2006 and 2006–2007, respectively. The total of air-freezing degree-days per year was confirmed to be the best and sufficient predictor for all considered thermal characteristics in the lower part of the talus slopes. Persistency of cold talus thermal behavior supports Nekola's concept of paleorefugia inhabited by cold-adapted species of boreal origin. Our results suggest that the talus microclimate can be sufficiently resistant to an increase of mean annual atmospheric temperature by 3 °C, retaining a sufficient number of freezing days during the winter season.

### Introduction

In central Europe, which has a temperate climate, some low-altitude stony accumulations feature a limited area of cold microclimate at their lower margin (Balch 1900, Wakonigg 1996, 2006, Gude *et al.* 2003, Zacharda *et al.* 2005, 2007). Due to their specificity, such talus slopes are inhabited by isolated populations of boreal and alpine plants and invertebrates (Růžička 2011, Růžička *et al.* 2012). Similarly, in north-eastern Iowa, alfic talus slopes also harbour populations of boreal invertebrates. Based on testing theoretical predictions, Nekola (1999) characterised these cold-retaining habitats as

paleorefugia. Due to the microclimatic buffering provided by cold-air seepage, which mimics the full-glacial regional climate, populations were able to persist in such refugia throughout the Hypsithermal period of the Holocene until the cooler and wetter conditions of modern times prevailed. The aim of this study was to investigate the interplay between the ambient meteorological and internal thermal talus characteristics, to verify and support, or to reject Nekola's concept of paleorefugium.

The meteorological conditions in central Europe fluctuated remarkably during the period 2003–2008, when contrasting below-average as well as above-average climatic variations



**Fig. 1.** Study sites. **(A)** Klíč Mount, the arrow indicates the area with a cold microclimate. **(B)** Kamenec, the area with a cold microclimate lies 10 m under the picture margin. **(C)** Suchý Vrch, gathering of data in humanly accessible subterranean spaces among rocky blocks covered with ice.

occurred. Some of the thermal deviations even exceeded the data from the entire history of the instrumental temperature measurements in the Czech Republic (Sandev 2007). Due to this variation in meteorological characteristics, we can analyse the response of the thermal regime in talus slopes to variations in air temperature, to obtain support for predicting the fate of these microclimatic conditions under future climatic parameters.

## Material and methods

### Study sites

Temperature measurements were carried out on three talus slopes in the České Středohoří upland and the Lužické Hory Mountains, North Bohemia (Czech Republic). The region is underlain by Cretaceous sediments consisting of marlite, claystone and sandstone, through which volcanic basalts and phonolites penetrated during the Tertiary. In all three localities, an area with a cold microclimate — an “ice hole” sensu Gude *et al.*

(2003), or a “cold air trap” sensu Edenborn *et al.* (2012) — is formed at the base of the talus slope. The sites are as follows:

**Klíč Mount** (50°47'N, 14°34'E): the southwest-facing phonolite talus slope (Fig. 1A) is composed of rockfall- and weathering-derived boulders 40–80 cm in diameter. The area of cold microclimate is situated at its base (540 m a.s.l.) and is covered by lichens and mosses, whereas the surface of most of the scree slope is bare. The cold low part of the scree slope was investigated geophysically, the blocky layer's thickness was estimated to be 10 m, and small ice lenses were inferred (Gude *et al.* 2003).

**Kamenec** (50°42'N, 14°21'E): a north-facing talus slope (Fig. 1B), derived from mechanical weathering of a basalt plateau. The strip of cold microclimate is located at its base (300 m a.s.l.), where bedrock boulders 40–80 cm in diameter are densely covered by non-vascular plants. The blocky layer's thickness was estimated using geophysics to be 10 m (Gude *et al.* 2003).

Suchý Vrch (50°49'N, 14°38'E): the northern slope of the hill is covered by large phonolite blocks, whereas the upper part of the slope is bare. The fissure-talus ice cave (called Naděje Cave) is situated in the forested part, at an altitude of about 580 m a.s.l. (Fig. 1C). The fissure is 30 m long, 1.8–3.5 m wide, and about 6-m deep, with a roof composed of large blocks (Zacharda *et al.* 2007).

The climate of the region is temperate, with a mean annual atmospheric temperature of 6–8 °C, and typical January and July mean air temperatures of –3 °C and 16 °C, respectively. Annual mean precipitation measured at nearby weather stations totals 600–750 mm. Precipitations occur irregularly in various seasons of the year, and enter the frozen talus both to form ice, and at the same time, act as an input of heat that can influence length of the zero curtain period.

## Temperature measurements

Data-loggers (Model TGU-0050, Gemini Data Loggers Ltd., Chichester, UK) with internal thermistors (accuracy  $\pm 0.2$  °C) were used to register the temperature every 3 h from December to November in the following year, for five consecutive years between 2003 and 2008. The registered data were downloaded yearly using the Gemini Logger Manager ver. 2.3, software. Ambient air temperature was measured by a shaded logger hanging about 2.5 m above the scree surface at the foot of the scree slope. Internal temperature was measured among stones at depths of 50–70 cm in the basal parts of Kamenec and Klíč talus slopes, and among stone blocks at a depth of about 6 m under the surface in the Naděje Cave on Suchý Vrch.

## Environmental characteristics

Based on the field measurements, 10 thermal characteristics were calculated, belonging to two different groups.

The following six talus characteristics (TC) of the inner environment at the base of talus slope were calculated:

MAIAT = mean annual internal air temperature.  
MaxIAT = maximum internal air temperature in the relevant year.

ITH = total of internal-temperature thawing degree-days per year.

IFR = total of internal-temperature freezing degree-days per year.

IID = total of internal ice days per year (days on which the maximum internal air temperature does not rise above 0 °C).

ZCD = total of zero-curtain days (the number of days with an internal temperature near 0 °C, as the near-surface ice melts). Days when the temperature began to be almost constant about in interval of –0.6 to 0 °C, and subsequently exceeded 0 °C, were considered the beginning and end of the ZC, respectively.

Four meteorological characteristics (MC) of ambient atmosphere were calculated:

MAAT = mean annual atmospheric temperature.  
MinAT = minimum atmospheric temperature in the relevant year.

ATH = total of air-temperature thawing degree-days per year.

AFR = total of air-temperature freezing degree-days per year.

The temperature data-loggers registered the sum of 24 degree-hours per day. The sum, divided by 24, provided a value of degree-days. A negative value was recorded as freezing degree-days, while a positive value was recorded as thawing degree-days. This cumulative index is a measure of both duration and magnitude of below-freezing (or above-thawing) temperatures during a specified period.

## Data analysis

Characteristics representing the sum of degree days or counts of days (i.e., ATH and AFR in the MC group, and ITH, IFR, IID and ZCD in the TC group), were log-transformed to homogenise their variation and linearise their relationship with other characteristics. Additionally, the log-transformation enabled us to set up the more natural model of the multiplicative relation between

the characteristics using additive linear statistical models.

The relationship between talus characteristics (TC) and meteorological characteristics (MC) was tested within a constrained linear ordination framework (redundancy analysis, RDA) using a Monte Carlo permutation test (ter Braak and Šmilauer 2012). The TC were used as the response variables and MC as the explanatory variables. The relationship among characteristics within the TC group and between the TC and MC groups was visualised using a biplot diagram. Using the RDA framework, we also analysed the predictive power of individual MC and the overlap in their predictive ability, comparing their independent (simple) effects with their conditional effects quantified during the stepwise selection both for the whole group of TC and for its individual members. Only those MC with independent effects that were significant at Type one error threshold value  $\alpha = 0.10$  were considered during stepwise selection. All the permutation tests performed in the RDA framework took into account the location as a random effect (location identity served as a covariate and the random permutations were restricted within each location) and the temporal autocorrelation between years (permutations were restricted for time series, *sensu* ter Braak and Šmilauer 2012).

As the evaluation of independent and conditional effects required tests of multiple related hypotheses using the same (set of) response variable(s), we applied family-wise corrections of the Type I error estimates, by transforming them into False Discovery Rate (FDR) estimates (Benjamini and Hochberg 1995). Analyses described in this paragraph were performed using the Canoco 5.0 software (ter Braak and Šmilauer 2012).

We also fitted predictive models for selected TC, which enabled us to predict TC values using a subset of MC that were found to be sufficient predictors during the stepwise selection. We used linear mixed-effect models with the location identity as a random effect and modelled temporal autocorrelation among yearly observations within each location using an autoregressive function of the first order (Pinheiro and Bates 2000). The linear mixed-effect models were fitted using library *nlme* and the graphs were plotted using *effects* library. Both libraries are parts of the R software (R Development Core Team 2012).

## Results

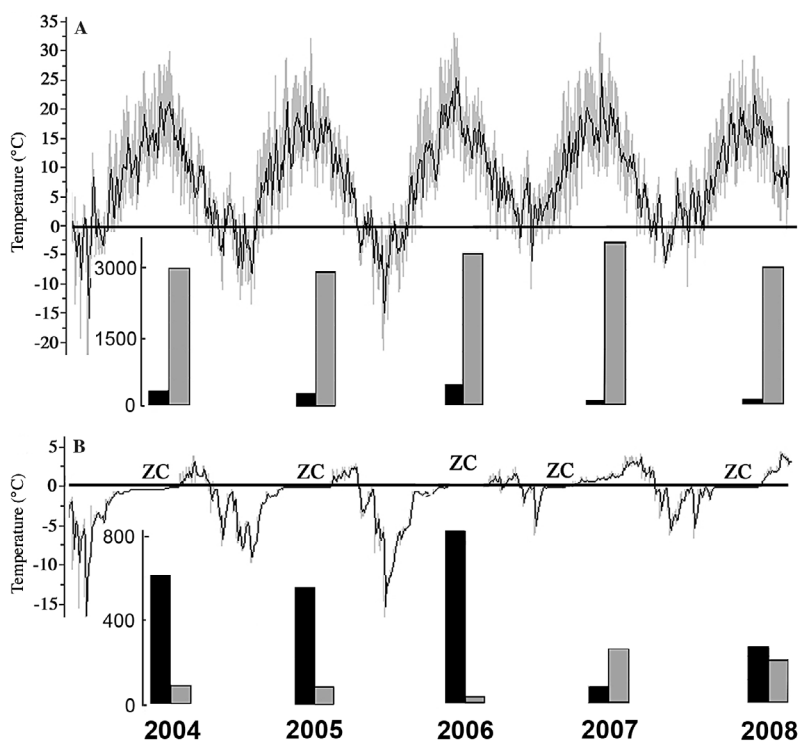
We recorded a wide range of values for all meas-

**Table 1.** Thermal characteristics. MAIAT = Mean annual internal air temperature, MaxiAT = Maximum internal air temperature, ITH = Total of internal-temperature thawing degree-days per year, IFR = Total of internal-temperature freezing degree-days per year, IID = Total of internal ice days per year, ZCD = Total of zero-curtain days. MAAT = Mean annual atmospheric temperature, MinAT = Minimum atmospheric temperature, ATH = Total of air-temperature thawing degree-days per year, AFR = Total of air-temperature freezing degree-days per year.

Study site and season	MAIAT	MaxiAT	ITH	IFR	IID	ZCD	MAAT	MinAT	ATH	AFR
Kamenec 2003/04	-1.54	3.9	104.73	668.05	276	123	7.53	-22.3	3045.02	294.47
Kamenec 2004/05	-1.43	2.8	95.66	618.71	291	127	7.45	-13.6	3026.15	306.31
Kamenec 2005/06	-2.10	2.3	35.86	803.68	319	128	7.68	-21.6	3208.89	401.92
Kamenec 2006/07	0.58	4.1	309.73	95.49	142	85	9.04	-10.9	3362.71	59.54
Kamenec 2007/08	-0.13	4.4	235.78	284.30	268	116	8.30	-10.7	3162.41	131.84
Klíč 2003/04	-0.11	8.0	449.40	491.32	264	115	6.78	-14.8	2833.60	355.66
Klíč 2004/05	-0.44	5.1	304.95	466.18	232	124	6.76	-13.9	2853.70	384.03
Klíč 2005/06	-0.90	6.7	390.75	722.80	236	105	6.96	-20.7	2999.25	457.20
Klíč 2006/07	1.98	8.0	830.99	104.84	110	64	7.89	-9.1	3006.23	125.71
Klíč 2007/08	1.69	7.5	808.62	188.87	156	86	6.99	-8.5	2784.41	230.55
Suchý Vrch 2003/04	-0.97	2.1	67.20	424.19	287	134	5.86	-14.8	2555.58	415.04
Suchý Vrch 2004/05	-0.69	3.4	112.01	365.92	290	146	6.00	-14.2	2630.60	437.75
Suchý Vrch 2005/06	-1.24	1.6	53.30	508.11	318	179	6.18	-20.0	2791.46	534.90
Suchý Vrch 2006/07	1.52	4.6	589.65	32.01	107	70	7.27	-9.9	2776.96	121.49
Suchý Vrch 2007/08	0.10	5.7	223.78	187.07	223	73	6.73	-9.9	2692.04	233.63



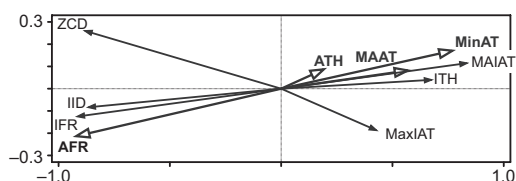
**Fig. 2.** Variations in temperature and selected environmental characteristics at Kamenec from December 2003 to November 2008. **(A)** Gray line presents daily variations of atmospheric temperature, black line connects daily mean values of atmospheric temperature. Total of air-temperature freezing degree-days per year (AFR, black columns), and total of air-temperature thawing degree-days per year (ATH, grey columns). **(B)** Variations in internal temperature, total of internal-temperature freezing degree-days per year (IFR, black columns), and total of internal-temperature thawing degree-days per year (ITH, grey columns); ZC = zero-curtain period.



ured characteristics (Table 1). For example, the mean annual atmospheric temperature registered at the three investigated localities fluctuated during five years between 5.86 and 9.04 °C. The annual total of air-temperature freezing degree-days ranged between 59.54 and 534.90 (Fig. 2).

The four MC explained 88.9% of the total variation in TC values in RDA. The biplot ordination diagram summarises the correlation among TC as well as the joint effects of MC predictors (Fig. 3). Characteristics IID, IFR and ZCD were positively correlated with the AFR characteristic, which appears to be the strongest predictor (based on its arrow length). The MAIAT, ITH and MaxIAT were negatively correlated with the AFR. The relationship between TC and the other three MC (ATH, MAAT, MinAT) was opposite to that of their relationship to AFR, but weaker, particularly for ATH.

The total air-temperature freezing degree-days (AFR) characteristic had the strongest independent effect (Table 2, Independent Effects part). The MAAT and MinAT characteristics also showed a significant explanatory power (and relatively large percentage of variation explained),



**Fig. 3.** Biplot diagram of RDA, using six talus characteristics (TC) as response variables (arrows with filled heads) and four meteorological characteristics (MC) as explanatory variables (arrows with empty heads). The MC explained 88.9% of the total variation in TC and of this, the first (horizontal) axis explained 95.2% and the second (vertical) axis another 3.6%. The arrows point in the direction of steepest increase of the respective characteristic values and the angles between arrows approximate correlations among TC and between TC and MC: linear correlation ( $r$ ) is approximated by the cosine of the angle, hence the arrows pointing into opposite directions correspond to characteristics with  $r$  approaching  $-1$ , while the arrows pointing in the same direction correspond to characteristics with  $r$  approaching  $+1$ . Acronyms of individual characteristics are explained in the Methods' section 'Environmental characteristics'.

but their conditional effects were negligible, revealing a large overlap in their explanatory

power with AFR (Table 2, Conditional Effects part).

Similar patterns were also found when testing the effect of MC on individual TC (Table 3); AFR always had the largest (and significant) independent effect, followed by MAAT and MinAT, whereas ATH had no significant effect and explained a very small part of the variation for individual TC. During stepwise selection, the AFR characteristic was found to be a sufficient predictor for values of all TC; after its addition to a model, the other MC had no significant conditional effect.

The fitted linear mixed-effect models revealed strong positive relations between AFR values and the IFR, IID and ZCD characteristics (Table 4, Fig. 4A for IFR) and similarly strong, but negative relations between AFR values and the values of MAIAT, ITH and MaxIAT characteristics (Table 4, Fig 4B for MAIAT). The regression equations (Table 4) can be used to predict the individual TC values based on AFR data.

Additionally, we fitted an alternative linear mixed-effect model to predict the number of zero-curtain days (ZCD) from the mean annual temperature (MAAT), to interpret our results in the context of predicted climate change. The effect of MAAT was highly significant ( $F_{1,11} = 24.7$ ,  $p < 0.001$ ) and the predictive equation is  $ZCD = \exp(7.615 - 0.4141 \times MAAT)$ . The fitted relationship is illustrated in Fig. 5A (B displays the relationship between MAAT and MAIAT characteristics). The value of the MAAT regression coefficient in the model predicting ZCD suggests that with each increase in the mean annual air temperature by 1 °C, the count of zero-curtain days is reduced by 34%. An increase in MAAT by 3 °C therefore, results in a reduction of ZCD to 29% of the present day count.

Discussion and conclusions

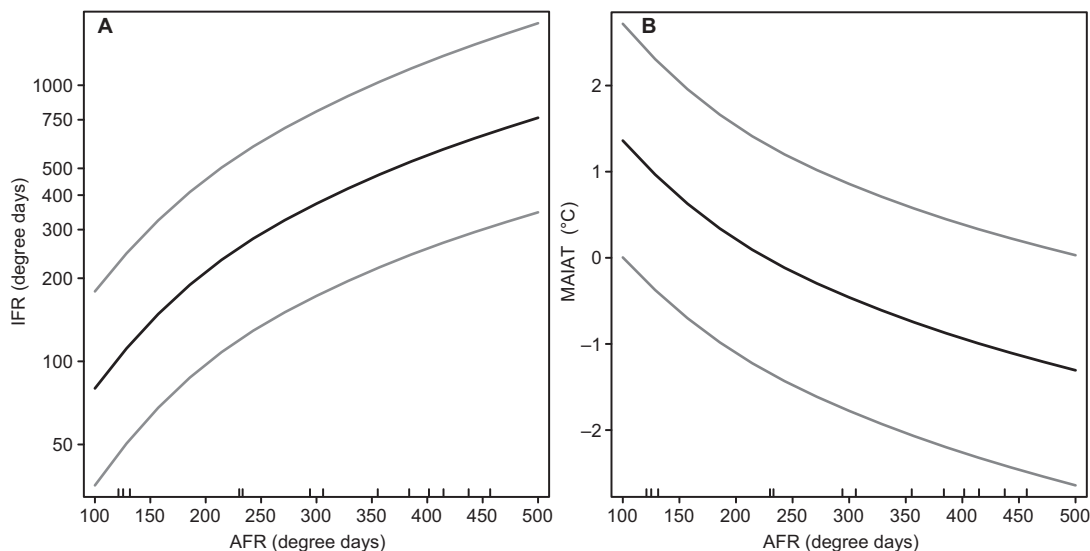
The AFR characteristic proved to be the most

**Table 2.** Independent and conditional (stepwise-selection based) effects of meteorological characteristics (MC) in a constrained ordination (RDA) using all six talus characteristics as response variables. Pseudo-*F* represents the test statistic used in the Monte Carlo permutation test, where  $p_{adj}$  represents the false discovery rate estimate. AFR = Total of air-temperature freezing degree-days per year, MAAT = Mean annual atmospheric temperature, MinAT = Minimum atmospheric temperature, ATH = Total of air-temperature thawing degree-days per year, n.s. = not significant.

Independent effects				Conditional effects			
	Explains (%)	Pseudo- <i>F</i>	$p_{adj}$		Explains (%)	Pseudo- <i>F</i>	$p_{adj}$
AFR	80.2	44.7	0.004	AFR	80.2	44.7	0.006
MAAT	71.0	26.9	0.002	MinAAT	0.9	0.5	n.s.
MinAT	53.3	12.6	0.002	MAAT	0.6	0.3	n.s.
ATH	15.2	2.0	n.s.				

**Table 3.** Independent effects of meteorological characteristics (MC) in a constrained ordination (RDA) using one of the talus characteristics (TC) as a response variable. The RDA with a single response variable effectively corresponds to a classical linear model, but the chosen permutation options take into account the effect of location and temporal autocorrelation. Each column shows results for a single TC, with the percentage of explained variation followed by an adjusted significance value [false discovery rate (FDR) estimate in parenthesis]. The FDR estimates > 0.10 are shown as not significant (n.s.). The order of MC in rows corresponds to decreasing explanatory power, with the exception of results for MAIAT, where MinAT explained slightly more variation than MAAT. The acronyms of MC and TC are explained in the Methods' section 'Environmental characteristics'.

	IFR	IID	ZCD	MAIAT	ITH	MaxIAT
AFR	92.3 (0.004)	83.7 (0.006)	69.7 (0.009)	89.5 (0.004)	81.5 (0.004)	42.2 (0.057)
MAAT	82.2 (0.002)	78.4 (0.002)	67.7 (0.009)	71.4 (0.003)	65.7 (0.002)	35.8 (0.073)
MinAT	58.9 (0.002)	43.3 (0.017)	44.9 (0.010)	72.7 (0.003)	59.4 (0.002)	32.5 (0.057)
ATH	20.9 (n.s.)	23.8 (n.s.)	13.7 (n.s.)	10.2 (n.s.)	9.1 (n.s.)	2.1 (n.s.)



**Fig. 4.** Relationship of **(A)** the total internal-temperature freezing degree-days per year (IFR) and **(B)** mean annual internal temperature (MAIAT) to the total air-temperature freezing degree-days per year (AFR), fitted by linear mixed-effect models. Each plot displays the fixed effect of AFR (thick black line) together with 95% confidence regions (gray lines). The upward tick marks on the x-axes represent the observed AFR values.

important predictor (and possibly driving force) of the majority of the thermal TC. In contrast, ATH did not influence the TC significantly and explained a very small part of their variation (Tables 2 and 3).

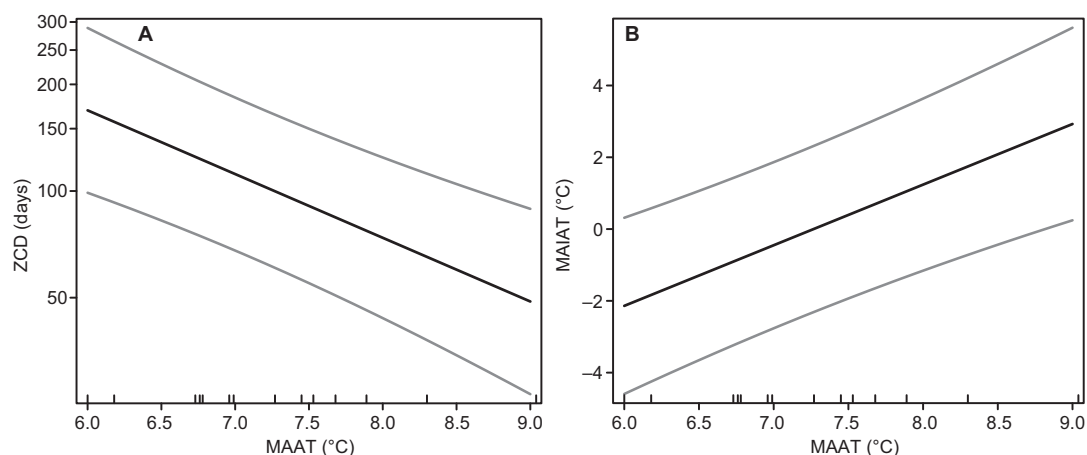
Why the increase in ATH does not lead to warming of the internal talus environment might be explained by the latent heat that is consumed during interstitial ice melt, and particularly by the existence of a thermally protective surface layer of talus (Zacharda *et al.* 2007). Růžicka

(1990) and Růžicka *et al.* (1995) registered distinctive daily fluctuations in temperature at the talus surface, whereas the temperature was nearly constant at 1 m below the insulating surface.

Temperature variations in talus slopes with ice formation have already been documented in limestone, sandstone, and conglomerate bed-rock areas at altitudes between 210 and 2600 m a.s.l., where the period of isothermal zero-curtain was reported to last usually 1.0–2.5 months

**Table 4.** Summary of fitted linear mixed-effect models using the total of air-temperature freezing degree-days (AFR) as an explanatory variable and each of the talus characteristics as a response variable in individual models:  $b_0$  is the intercept estimate,  $SE_0$  is its standard error,  $b_1$  is the estimate of regression coefficient for (log-transformed) AFR,  $SE_1$  is its standard error,  $F$  is the  $F$  statistic for the test of AFR effect ( $df = 1, 11$ ),  $p$  is the corresponding significance of the AFR effect. An asterisk following a talus characteristic (TC) name indicates that the response variable was log-transformed. Values of an individual TC can be predicted using known AFR values, based on  $b_0$  and  $b_1$  values by the equations  $TCX = \exp[b_0 + b_1 \times \ln(\text{AFR})]$  and  $TCX = b_0 + b_1 \times \ln(\text{AFR})$  for the TC with and without asterisk, respectively.

	IFR*	IID*	ZCD*	MAIAT	ITH*	MaxIAT
$b_0$	-2.0780	2.2271	2.6959	8.9903	11.4175	12.4494
$SE_0$	0.7738	0.3727	0.3724	1.0720	0.9992	2.6811
$b_1$	1.4023	0.5793	0.3552	-1.6568	-1.0985	-1.4086
$SE_1$	0.1238	0.0616	0.0647	0.1588	0.1511	0.4258
$F$	128.2	88.4	30.1	108.9	52.9	10.9
$p$	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.007



**Fig. 5.** Relationship of **(A)** the total zero-curtain days per year (ZCD), and **(B)** mean annual internal temperature (MAIAT) to mean annual atmospheric temperature (MAAT), fitted by linear mixed-effect models. Each plot displays the fixed effect of MAAT (thick black line) together with 95% confidence regions (grey lines). The upward tick marks on the x-axes represent the observed MAAT values.

(Wakonigg 1996, 2006, Lambiel and Pieracci 2008, Delaloy *et al.* 2010, Edenborn *et al.* 2012). In contrast, the isothermal zero-curtain period in taluses in North Bohemia lasts about four months.

The formation and persistence of ice at the lower margin of talus slopes might be influenced by numerous factors (Růžicka 1999). A concave foot of slope formed by large boulders was the major factor inducing thermal anomaly (Delaloy *et al.* 2003, Raska *et al.* 2011). Slope topography and various types of mass movements (e.g. bulging, creep, landslides or their combination) result in the formation of depressions at the base of talus slopes in the region. Basalt and phonolite exhibit high values of compressive strength (Hoek 1994) and can form deep accumulations, in which the material at the bottom (stones of between 30–70 cm in size) does not crush under the pressure of overlying stones. The depth of the stony layer with large air voids reaches up to 10 m, as measured by geophysical methods. The coincidence of such geology, geomorphology and a low-altitude location — where no or only a thin thermally insulating snowpack occurs — results in extraordinary overcooling and to the long persistence of ice in taluses in North Bohemia (Růžicka *et al.* 2012).

The collection of spiders and mites along almost the whole altitudinal gradient (400–

1600 m a.s.l.) in the Czech Republic revealed that the occurrence of cold-adapted species depends on the existence of thermally-buffered cold microclimate sites (Růžicka and Klimeš 2005, Zacharda *et al.* 2005, Růžicka and Zacharda 2010, Růžicka 2011). Dobrowski (2011) has designated these places as microrefugia, and asked where they might occur and has also suggested that “there is little explicit understanding of the climatic processes that would allow for microrefugia to exist”. However, not only climatic processes, but also landscape relief, altitude, sun exposure, vegetation cover and the velocity of air fluxes can participate in the formation of local microclimate. Here, the question arises: what might be a boundary value of the increase in atmospheric temperature to be tolerated by talus-inhabiting psychrophilic species to survive?

In the period 2006–2007, with a higher than normal winter temperature, the values of AFR and MAAT were 60 and 9 °C, respectively, on the Kamenec. This corresponds to an increase in the mean annual atmospheric temperature of 2 °C in comparison with the long-term mean annual atmospheric temperature. Nevertheless, the inner environment at the base of the talus slope was characterised by the following values: IFR = 95, MAIAT = 0.6 °C, ZCD = 85. The length of the zero curtain was longer than two months (Table 1 and Fig. 2).



Climate warming is increasing the dominance of warm-adapted species — a process described as “thermophilisation”. De Frenne *et al.* (2013) documented significant thermophilisation of understory vegetation in European and North American temperate forests. Using the Aladin regional climate model for the Czech Republic (Farda *et al.* 2010), and following the A1B scenario of projected future climate (Nakićenović 2000), climatologists estimate the MAAT increase to be 3.3 °C in the years 2070–2099 in the Czech Republic (compared with the reference period 1961–1990). Within the same period, the annual total number of frost and ice days is expected to decrease, but never to zero (IPCC 2013).

Multiple sources report a positive deviation of 1–3 °C from the recent mean for various areas of temperate zone during the Atlantic period, the Holocene climatic optimum (Anderson *et al.* 2007). The carbonate algific talus slopes studied by Nekola (1999) in northeastern Iowa, as well as the volcanic talus slopes in North Bohemia might maintain an autonomous cold microclimate and represent typical palaeorefugia. Our observations confirm the strong potential for the continuity of disjunct psychrophilic populations at such sites since glacial times. Based on our data, we can justifiably suppose that even such an extent of warming in the future (increase of MAAT by 3 °C) will not endanger the cold talus ecosystems.

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